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Reconstructing the reproductive mode of an Ediacaran macro-organism

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Enigmatic macrofossils of late Ediacaran age (580–541 million years ago [Ma]) provide the oldest known record of diverse complex organisms on Earth, lying between the microbially-dominated ecosystems of the Proterozoic and the Cambrian emergence of the modern biosphere.¹ Among the oldest and most enigmatic of these macrofossils are the Rangeomorpha, a group characterized by modular, self-similar branching and a sessile benthic habit.^{2,3,4} Localized occurrences of large *in situ* fossilized rangeomorph populations allow fundamental aspects of their biology to be resolved using spatial point techniques.⁵ Here, we use such techniques to identify recurrent clustering patterns in the rangeomorph *Fractofusus*, revealing a complex life history of multigenerational, stolon-like asexual reproduction, interspersed with dispersal of waterborne propagules. Ecologically, such a habit would have allowed for both the rapid colonisation of a localized area and transport to new, previously uncolonized areas. The capacity of *Fractofusus* to derive adult morphology via two distinct reproductive modes documents the sophistication of its underlying developmental biology.

Late Ediacaran sedimentary strata (~580–541Ma) of Newfoundland and the UK are dominated by rangeomorphs, whose unique self-similar branching construction³ makes resolution of their phylogenetic relationships, or even their basic biology, difficult.¹ The occurrence of rangeomorphs in conspicuously deep-water sediments has led to a general consensus that they were heterotrophic,⁶ while the global distribution of charniids (a rangeomorph sub-group) has been interpreted as evidence for reproduction via waterborne propagules.⁷ In the present study we use spatial statistics and modelling^{5,9} in a novel approach to illuminate the reproductive biology and underlying ecology of one of the most abundantly-preserved rangeomorph fossils, *Fractofusus*.⁸

We analysed three large bedding-plane assemblages of *Fractofusus* in SE Newfoundland: 1) the ‘D’ surface and 2) the ‘E’ surface at Mistaken Point, Avalon Peninsula;^{8,10} and 3) the H14 surface on Bonavista Peninsula (locality 14 of Hofmann et al.)¹¹ (Extended data Fig. 1a-c). A volcanic tuff directly above the ‘E’ surface has been dated to 565 ±3 Ma,¹² which also constrains the age of the underlying ‘D’ surface. Regional lithostratigraphic correlations suggest that the H14 surface is a few million years younger than the Mistaken Point beds.¹¹ All three assemblages occur within deep-marine turbidite sequences, with *Fractofusus* fossils preserved as negative epirelief external moulds in siltstone hemipelagites, cast from above by volcaniclastic deposits.⁶

Fractofusus is conspicuously endemic, restricted almost exclusively to southeastern Newfoundland,¹³ where it dominates many macrofossil assemblages.¹⁰ *Fractofusus* has a rounded, elongate spindle-like morphology, with two (arguably three^{2,13}) offset rows of irregularly alternating, self-similar, subdivided frondlets arranged along a central axis.^{2,14} *Fractofusus* specimens range from 1cm to 42cm in length² (Fig. 1a,b); two species have been

described, distinguished by their length:width ratios.² The ‘D’ and ‘E’ surfaces are dominated by the elongate form, *Fractofusus misrai* (L/W=3.2, Fig. 1a), whereas the more ovate *Fractofusus andersoni* (L/W=1.6, Fig. 1b) dominates the H14 surface.¹⁰ *Fractofusus* occurs in dense benthic populations and exhibits no evidence of motility or current orientation.² Together with nearest neighbour spatial analyses,¹⁰ these observations point to a sessile, recumbent, benthic mode of life in aggregated communities.

The spatial positions of *Fractofusus* were mapped to millimetre-scale resolution using differentiated GPS (Extended data Figs. 1d-f) on the two surfaces at Mistaken Point, and by tracing specimen outlines onto acetate sheets at H14; significantly, this latter approach also allowed size data to be recorded (Extended data Fig. 1f). The ‘D’ and ‘E’ surface data were corrected for tectonic deformation prior to analysis (Extended data Fig. 2).⁷ Heterogeneous Poisson models were used to identify possible distortions arising from differential erosion of the bedding planes (Supplementary Table 1). Pair correlation functions (PCF) were calculated to describe the spatial distributions of taxa on each bedding plane.⁵ Monte Carlo simulations¹⁵ and Diggle’s goodness-of-fit test⁵ (the p-value p_d , where $p_d=1$ indicates a perfect model fit and $p_d=0$ indicates no fit), were used to compare the fit of different spatial models to the data (specifically homogeneous and heterogeneous Poisson models¹⁶ and single and double homogeneous and heterogeneous Thomas cluster models).¹⁶ PCFs were also used to describe the spatial distributions of taxa other than *Fractofusus* on the ‘D’ and ‘E’ surfaces. For the H14 surface, spatial relationships between three distinct *Fractofusus* size classes (defined in Methods, Extended data Figs. 3a,b) were analysed by calculating partial PCF⁵ and comparing model fit of bivariate shared parents models (SP) with linked cluster models (LCM).¹⁶ Finally, spatial directionality was investigated by plotting their generalised K-

functions¹⁷ from 0° to 360° (isotropy plots), allowing visualisation of the relative directional positions of specimens (Fig. 3).

Non-random spatial distributions of sessile organisms, i.e. those that do not exhibit complete spatial randomness (CSR), can be explained by either extrinsic factors (e.g. environmental heterogeneities), or intrinsic reproduction.¹⁸ Identifying the processes behind such patterns is not straight-forward; however, extrinsically-induced patterns are generally best modelled by heterogeneous Poisson models,¹⁸ which describe randomly distributed points with a non-uniform density across the sampled area. In contrast, intrinsic processes typically generate Thomas cluster models,¹⁸ where the points within each cluster have a normal density distribution centred on a parent point.

All three populations of *Fractofusus* were found to be significantly aggregated, conforming closely to homogeneous Thomas cluster models (Fig. 2a). Specimens on the ‘E’ and H14 surfaces are aggregated at two spatial scales, forming clusters of clusters (Fig. 2a,b). On the ‘E’ surface, this distribution is best modelled by a nested homogeneous double Thomas cluster model of 23 clusters (radius $r=0.242\text{m}$), each containing 12 smaller clusters ($r=0.074\text{m}$) of 3 specimens ($p_d=0.76$). The H14 surface distribution is best modelled by a nested homogeneous double Thomas cluster model of 24 large clusters ($r=0.237\text{m}$), each containing 6 clusters ($r=0.079\text{m}$) of 8 specimens ($p_d=0.89$). The ‘D’ surface distribution forms discrete clusters (not clusters of clusters), which are best modelled by a single Thomas cluster model ($p_d=0.77$) with 338 *Fractofusus* clusters of 3 specimens ($r = 0.086\text{m}$) (Extended data Tables 1–2). Importantly, the spatial distribution on the ‘E’ surface can also be modelled by the nested double cluster pattern found on the H14 surface (Fig. 2b) ($p_d^{HonE}=0.51$), strongly implying the same underlying process for both distributions (Fig. 2b,

Extended data Table 3). The spatial distribution of *Fractofusus* on the ‘D’ surface is conspicuously similar to that seen in the larger specimens on H14 (Extended data Fig. 4e). By contrast, the spatial distributions of other taxa – *Thectardis*, *Primocandelabrum* and *Charniodiscus* – exhibit fundamentally different magnitudes and spatial scales of aggregation, both to each other and to those of *Fractofusus* (Fig. 2b and Extended data Tables 4, 5).

The close fit of *Fractofusus* spatial distributions to single and nested double Thomas cluster models strongly suggests that they derive from reproductive rather than extrinsic (environmental) factors. Reproductive biology is further corroborated by size analysis of the *Fractofusus* population on the H14 surface (Fig. 2c, Extended data Figs. 4a,c,d), which reveals strikingly different spatial patterns for each of the three size classes (Fig. 2c, Extended data Tables 1–2). Whereas the largest size class (>11.0cm) is randomly distributed ($p_d=0.30$), both the intermediate (5.5–11.0cm) and smallest (<5.5cm) size classes are hierarchically clustered: small individuals cluster around intermediate individuals ($p_d^{LCM}=0.74$ versus $p_d^{SP}=0.03$; Extended data Table 5), which in turn cluster around large individuals ($p_d^{LCM}=0.66$ versus $p_d^{SP}=0.01$). In other words, the smallest specimens form clusters (homogeneous nested double Thomas cluster model ($p_d=0.72$)) around intermediate-sized specimens (homogeneous single Thomas cluster model; $p_d=0.51$), which are themselves clustered around randomly distributed large specimens (homogeneous Poisson model $p_d=0.31$; Figs. 2c, 4, Extended data Fig. 5, Extended data Tables 1–2). Moreover, the isotropy plots for H14 (Fig. 3) show strong directionality for the large size class, but limited directionality for the medium and small size classes. The nested clusters on the ‘E’ and H14 surfaces suggest three generations, while the single clusters on the ‘D’ surface suggest two, reflecting an earlier stage in population development. The difference is consistent with the

suggestion that the ‘D’ surface records an earlier stage in the ecological succession of Ediacaran macroscopic communities¹⁰ (SI:2:3).

As with other Ediacaran macrofossils, there is no direct fossil evidence of reproductive habits in *Fractofusus*, but its recurrent distribution on bedding surfaces provides a statistically robust approach for inferring the underlying processes.¹⁹ In modern oceans, large sessile organisms typically reproduce by means of waterborne propagules, fragmentation/budding, and/or stolons (i.e., production of asexual clones that are at least initially connected to the parent by specialized outgrowths).

Spatial distribution of waterborne propagules – including both sexual and asexual spores, as well as sub-millimetre buds and fragments – are a function of current and rate of sinking. Even with rapid sinking ($\sim 1\text{mm/s}$)²⁰ and slow currents ($\sim 1\text{cm/s}$), propagules released from the dorsal surface of a ‘parental’ *Fractofusus* ($\sim 2\text{--}3\text{cm}$ above the substrate) would have been current aligned²¹ and dispersed by decimetres or more.²² Slow descent times also correspond with right-skewed (mean greater than the median) density distributions.^{20,21} The random spatial distribution of the H14 largest size class likely reflects a large dispersal distance (Extended data Table 1), which coupled with its highly directional isotropy plot (Fig. 3a) indicates that the largest specimens were strongly influenced by currents (c.f. Darroch et al.^{7,10}) As such, they likely derive from waterborne propagules and represent the initial establishment of a *Fractofusus* population on this surface.

The hierarchically clustered bedding plane distributions of small and medium *Fractofusus* on H14 closely match patterns exhibited by organisms reproducing asexually via stolon-like lateral extensions (Extended data Fig. 5).²³ Cluster distributions of the small and medium

size classes are also highly left-skewed (median greater than the mean), with the mean distance from each “parent” to their “offspring” on the order of a few centimetres (Fig. 2a), and offspring exhibiting no significant directionality or current orientation (Fig. 3b–c, Extended data Fig. 3c). The reproducibility of the model distributions across the three bedding-plane assemblages further attests to the indifferent effects of current: the spatial distributions of non-tethered offspring would result in patterns dependent on current velocity, which are unlikely to be consistent across multiple bedding planes in different localities. Moreover, there are no recorded instances of buds or fragmentary specimens of *Fractofusus* in any of its 5000+ documented specimens^{1,10,11,24} (see SI:2.5, SI:3). As such, the *Fractofusus* clusters on the H14 surface are not consistent with waterborne propagules or fragmentation/budding, but are directly comparable to stolon-like reproduction. Other taxa exhibit an intriguing range of non-random habits, and our preliminary analyses indicate that *Primocandelabrum* and *Charniodiscus* may have also reproduced using stolons.

Reproductive biology lies at the core of ecological and evolutionary dynamics, and its positive identification in Ediacaran macrofossils has the potential to illuminate the beginnings of the modern marine biosphere. Previous studies of Ediacaran macrofossils have investigated the seasonality of reproduction⁷, identified putative stolons^{28,29}, and inferred sexual or asexual reproduction based on biogeographic distribution or qualitative description of local populations.^{7,10} In the case of phosphatized ‘embryo’ microfossils, internal cell packages have been interpreted as evidence of germ-soma differentiation,³⁰ but it remains to be seen how those fossils relate to the evolution of large and/or complex eukaryotes.

The identification in *Fractofusus* of a multigenerational asexual clonal phase, interspersed with the release of waterborne propagules, is the first statistically robust account of

reproductive life history reported in an Ediacaran macrofossil. Such a strategy would have allowed for the rapid exploitation of localized areas, as well as for transport to new, previously uncolonized areas. The conclusion that *Fractofusus* could switch between reproductive modes further reveals the sophistication of its underlying developmental programme, capable not only of tissue differentiation, but also the generation of new macroscopic individuals from both benthic stolons and waterborne propagules.

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273

274 **Author Contributions**

275 E.G.M conceived the project, collected data on the ‘D’ and ‘E’ surfaces and ran the analyses.
276 C.G.K, A.G.L and J.J. M collected data on the H14 surface. All authors discussed the results
277 and prepared the manuscript.

278

279 **Author Information**

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281 declare no competing financial interests. Correspondence and requests for materials should
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Figure 1: a, *Fractofusus andersoni* specimen from the H14 surface. **b,** *Fractofusus misrai* from the ‘E’ surface, showing a large size-class partial specimen (~20cm, above) alongside a small size-class specimen (3.5cm in length, below). Scale bars = 1cm. Photographs are unretrodeformed.

Figure 2: PCF for mapped taxa. For all plots the x-axis is the inter-point distance between organisms in metres. The y-axis PCF=1 indicate CSR, <1 indicates segregation, and >1 indicates aggregation. **a,** PCF for *Fractofusus* on the ‘D’ surface (1040 specimens), ‘E’ surface (1141 specimens) and H14 surface (1214 specimens). Grey shaded area depicts the bounds of 99 Monte Carlo simulations of CSR. Since the PCF curves are not completely within these areas, the CSR hypothesis is rejected and one can assume that the *Fractofusus* distributions on all three surfaces form cluster patterns ($p^D_d < 0.01$, $p^E_d < 0.01$, $p^{H14}_d < 0.01$). **b,** PCF for non-CSR ‘E’ surface taxa (charniid 76 specimens, *Charniodiscus* 326 specimens, *Primocandelabrum* 311 specimens and *Thectardis* 39 specimens). Grey shaded area depicts 99 Monte Carlo simulation of the best-fit H14 surface model of double Thomas cluster process. Note how the ‘E’ surface *Fractofusus* PCF follows the H14 surface PCF very closely, and can be modelled by the same process ($p_d = 0.51$). Other ‘E’ surface taxa have dramatically different PCF to the *Fractofusus* PCF. **c,** PCF for the three size classes of *Fractofusus* on H14 surface. Grey shaded area depicts the 99 Monte Carlo simulation of CSR. The large size-class (350 specimens) exhibits CSR ($p_d = 0.30$), the intermediate size-class (310 specimens) shows aggregation <0.10m (single Thomas cluster model ($p_d = 0.51$)). The small size-class (554 specimens) shows a large aggregation <0.08m and a lesser aggregation between 0.08m and 0.20m (double Thomas cluster model ($p_d = 0.72$)).

Figure 3. Isotropy plots from the H14 surface for each size class of *Fractofusus*, providing a visualisation of specimen positions relative to one another. The vertical axis on each

subfigure depicts the colour map of specimens/m² normalised to account for different densities between size-classes. A peak (<1) is shown in green or yellow and depicts clustering, while a dip (<1) is shown in blue and depicts segregation. If there are no directional effects then the colour map in every direction from the centre point should be similar. **a**, The large size-class shows strong anisotropy, with aggregation of up to 4 normalised specimens/m². In contrast the **b**, medium and **c**, small size-classes show isotropy, that is a relative evenness of aggregations with a maximum density variation up to 0.5 normalised specimens/m².

Figure 4: Schematic diagram showing simplified *Fractofusus* spatial arrangements. The actual number of clusters, and clusters within those clusters, is higher than shown (23 clusters each containing 12 clusters of 3 specimens on the H14 surface), making their direct visual detection challenging. No overlapping specimens are shown because, while the best-fit models allow for overlaps, the observed PCF between the small size-class (Extended data Fig. 4c,d) and the large size-class (Fig. 2b) shows a small segregation (<3cm) away from the model behaviour, and a similar, non-significant segregation for the large size-class.

Methods

Data collection

Fossil taxa³¹ and spatial positions on the Mistaken Point 'D' and 'E' surfaces (Extended data Figs. 1a,b, 2a,b) were recorded using differentiated GPS over a period of fifteen days. A fixed GPS transmitter was installed on a headland overlooking the bedding planes, and a portable GPS receiver was used to map 4496 individual fossils over a total area of 123.7m² for both surfaces (SI:2.1); the mean accuracy of data points was 0.4 ±0.06 cm horizontally and 0.82 ±0.11 cm vertically. The measured position of each specimen represents the mean of five separate GPS readings collected over five seconds; both the accuracy (standard deviation of

the five readings) and the associated weather conditions were recorded for each reading. Mann-Whitney tests were used to compare the densities of specimens recorded in differing weather conditions, with the null hypothesis that the density should not depend on the weather conditions on the day of data collection.

Fossil positions on the H14 surface, Bonavista Peninsula (Extended data Fig. 1d) were recorded by tracing the outline of each specimen onto 2m x 5m acetate sheets. Cleavage and other geological features were also traced. These data were collected by three people, two holding the sheets in position and the third recording the data. Wind-induced slippage (affecting large-scale spatial relationships (>0.75 m) for three out of five of the sheets) was determined by measuring the differences between cleavage features crossing sheets, yielding a mean accuracy of 1.47 ± 0.26 cm along strike, and 1.53 ± 0.08 cm parallel to dip. Over the 0.5m distance that the PCFs were calculated, these errors translate to 0.37 ± 0.26 cm along strike and 0.15 ± 0.08 cm parallel to dip – substantially less than the 1cm cells within which specimen densities were measured to calculate the PCFs (Methods section: Testing for non-random spatial distribution). The sheet approach was used to map the H14 surface because it provided size data more efficiently than direct measurement plus GPS.

Specimen identification

Specimens were recorded as one of twelve taxonomic groups of macrofossils, including two ‘bin’ groups.³² : 1) *Bradgatia*, 2) *Pectinifrons*, 3) *Thectardis*, 4) *Fractofusus andersoni* + *F. misrai*, 5) *Charniodiscus spinosus* + *C. procerus*, 6) “Feather Dusters”, 7) *Hiemalora*, 8) Ivesheadiomorphs,³³ 9) Lobate Discs, 10) *Charnia* ‘A’ + *Charnia* ‘B’ [*Charnia* ‘A’ consists of *Beothukis mistakenis*^{34,35} (which dominates the ‘E’ surface) and *Charnia masoni*. *Charnia* ‘B’ now reassigned as *Trepassia wardae*.³⁴ Charniid populations on Mistaken Point are dominated by *Beothukis* (only four individuals on the ‘E’ surface are true *Charnia*

species), therefore direct comparison of data from this grouping with those from other taxonomic groups should be undertaken with caution. 11) “Holdfast Discs” [all discoidal specimens of uncertain affinity, with or without associated stems, which lack sufficient detail to identify the taxon], 12) “Other Species” [rare forms that do not fall into any of the other groups; e.g., *Hapsidophyllas*].

Retrodeformation

The tectonically distorted data from the Mistaken Point surfaces were retrodeformed by returning elongated holdfast discs to a circular outline⁶ The ‘D’ surface (based on 13 specimens), showed a deformation factor of 1.35 ± 0.11 ($R^2 = 0.92$), and the ‘E’ surface (based on 12 specimens) 1.71 ± 0.08 ($R^2 = 0.754$), both within the previously measured range.¹⁰ In the absence of any obviously directional distortion or suitable deformation indicators, measurements taken from the H14 locality were not adjusted in this fashion.

Data Collection Bias

The impact of mechanical weathering on the ‘D’ and ‘E’ surfaces was investigated by modelling the fossil distributions as heterogeneous Poisson processes. Fossils were originally covered in a thin layer of volcanic tuff, which has since been partially weathered away to expose the bedding planes, potentially inducing bias. If the density of a particular taxon is correlated to modern weathering features, then such processes are likely to be masking the true palaeontological distribution of the fossils. Initial data exploration and residual analysis of weathering effects was performed in R³⁶ using the package spatstat.³⁷ Four covariates, corresponding to four potential erosion sources, were investigated:

1. Across the bedding plane (South to North) x , which is differentially eroded by cliff fall and water runoff from a small stream on the northern side for the 'E' surface.
2. Along the three bedding planes (West to East) y , which are subject to differential erosion from wave action.
3. The south-western corner xy , which is the first point of contact for most waves on the 'E' surface.
4. The height of the fossils above the troughs of the tectonic ripples on the 'D' and 'E' surfaces h , which is an inverse proxy for ash coverage.

On each bedding plane, and for each parameter, the spatial density of fossils in relation to the parameter was plotted, along with the best-fit quadratic line. This best-fit line was then used to model the change of density compared to the covariant. The inhomogeneous models were tested primarily on the non-retrodeformed data (since retrodeformation may mask any aggregation due to preservational bias), and verified by conducting similar tests on the retrodeformed data. Two different methods were used to compare the different inhomogeneous models: Kolmogorov-Smirnov tests were performed on quadrats of the data to investigate the distributions relative to the four covariates³⁸ (Supplementary Table 1), then the model fit was assessed using the model residuals.^{5,9} Model residuals assessed the fit of the model to the data via plotting Q-Q and smoothed residual plots. If the observed line in the Q-Q plot falls outside two standard deviations of the model, the model was rejected.^{5,9} Akaike information criterion (AIC) values³⁹ were used to compare the relative quality of the statistical models that fit the data.

Bias generated by differing light conditions was tested by comparing densities of areas either side of a specific grid line that delineated where one (the right hand) side was mapped under optimal conditions, and the other under sub-optimal conditions. Similar levels of ash

erosion existed on either side of this grid line, so we expected that similar fossil densities should be found on both sides if the weather did not affect data collection. The densities were then compared using a Mann-Whitney test.

Testing for non-random spatial distributions

Initial data exploration, inhomogeneous Poisson modelling and residual analysis were performed in R³⁷ using the package spatstat.³⁸ Programita⁴⁰ was used to find distance measures and to perform aggregation model fitting (described in detail in references 40-42). Pair correlation functions (PCF) was used to assess which did not exhibit CSR, where PCF value reflects how many times more likely the distribution seen is aggregated (or segregated) compared to CSR as follows:

1. A distribution map was plotted for individual taxa, with the surfaces split into a grid of 1cm x 1cm cells, within which the population density was calculated.
2. The smoothed PCF was calculated with smoothing dependent on number of specimens for each taxon. A three cell smoothing was applied for *Fractofusus* (D, E and H14), five cells for *Charniodiscus* (E), *Pectinifrons* (D), *Bradgatia* (D and E) and *Primocandelabrum* (E) and 15 cells for *Thectardis* (E) and Charniids (D and E).
3. 99 simulations were run for each taxon on a homogeneous background to generate simulation envelopes around the random (PCF = 1). 99 simulations were run (instead of 100, for example) so that the p_d values could be measured in 0.01 increments.
4. p_d values were calculated using Diggle's goodness-of-fit test.¹⁵

For those taxa found to exhibit excursions outside the simulation envelope, four types of processes were then fitted to the data: heterogeneous Poisson process, Thomas single cluster

processes on both homogeneous and heterogeneous backgrounds, and Thomas double cluster process. The resulting models were then compared to find the best model for each taxon

Complexities of assessing model fit

Testing for significance with spatial point data is more complicated than for classical statistics due to lack of independence and variety of point pattern distributions⁴. Monte Carlo simulations provide a good assessment, but the simulation envelope does not necessarily correspond to a confidence interval,¹⁵ and runs the risk of Type 1 error if the observed PCF falls near the edge of the simulation envelope.¹⁵ The size of simulation envelopes depends on the sample size, so that smaller sample sizes (such as the H14 large size class of 350 specimens) has a relatively large simulation envelope in contrast to the ‘D’, ‘E’ and H14 surfaces (all >1000 specimens). A comparatively large simulation envelope reduces the likelihood that the null model (such as CSR) is rejected. Consequently, hypothesis testing needs to be further supplemented. We used Diggle’s goodness-of-fit test, which is a single test statistic¹⁵ (p_d) representing the total squared deviation between the observed pattern and the theoretical result across the studied distances. p_d was used in conjunction with visual inspection of Monte Carlo simulations for two reasons. First, p_d does not strictly test whether a model should be accepted or rejected, but whether the PCF for the observed data is within the range of the stochastic realization of the model.⁴³ Secondly, p_d depends on the range over that it is calculated. For example, the model which best describes the ‘E’ surface data has $p_d=0.56$, which may appear low. However, inspection of the PCF (Extended data Fig. 3b) shows a very close fit to the double Thomas cluster model above 2cm (Extended data Table 2). The finite size of *Fractofusus* is reflected in the lower PCF values at small distances, and so the model is only fit >2cm.

Interpreting ecological processes from spatial point patterns is imprecise. Different processes can produce similar spatial patterns,^{9,18,44,45} with the complex interplay of intra- and interspecific interactions affecting organismal distributions.^{46,47,48} Even so, application of complementary statistical techniques, such as pair correlation functions (PCF) combined with comparisons of inhomogeneous Poisson and Thomas cluster models, and nearest neighbour distance analysis, offers the most effective means of teasing out the underlying ecological processes.

Model fitting

If a taxon was not randomly distributed on a homogeneous background (Extended data Table 1), the random model on a heterogeneous background was tested. Six different heterogeneous backgrounds were generated, as follows (Extended data Table 4):

1. The first heterogeneous background was created from the density map of the taxon under consideration, being defined by a circle of radius R over which the density is averaged throughout the sample area. Density maps were formed using estimators within the range of $0.1\text{m} < R < 1\text{m}$, and the R corresponding to the best-fit model was used.
2. The second heterogeneous background was created from density maps of all specimens on each surface combined.
3. The third to sixth heterogeneous backgrounds were created from the four separate density maps of *Fractofusus*, *Ivesheadiomorphs*, *Charniodiscus* and *Primocandelabrum*.

This procedure follows that used to test for a non-random distribution on a homogeneous background (Section: Testing for non-random spatial distributions), except at point 3, where

the homogeneous background on which the taxa were simulated is replaced by a heterogeneous one. If excursions outside the simulation envelopes for both homogeneous and heterogeneous Poisson models remained, then cluster models were fitted to the data. For each non-random taxon, univariate cluster models were fitted as follows (Extended data Table 1):

1. The PCF and L function⁴⁹ of the observed data were found. Both measures were calculated to ensure that the best-fit model is not optimized towards only one distance measure, and thus encapsulates all spatial characteristics.
2. Best-fit Thomas cluster processes⁵⁰ were fitted to the two functions where $PCF > 1$. The best-fit lines were not fitted to fluctuations around the random line of $PCF = 1$ in order to aid good fit about the actual aggregations, and to limit fitting of the model about random fluctuations. Programita used the minimal contrast method^{9,15} to find the best-fit model.⁹
3. If the model did not describe the observed data well, the lines were refitted using just the PCF. If that fit was also poor, then only the L-function was used.
4. 99 simulations of this model were generated to create simulation envelopes, and the fit checked using the O-ring statistic.⁴⁰
5. p_d was calculated over the model range. Very small-scale segregations (under 2cm) were not included in the model fitting, since they likely represent the finite size of the specimens, and the lack of specimen overlap.
6. If there were no excursions outside the simulation envelope and the p_d -value was high, then a univariate homogeneous cluster model was interpreted as the best model.

Taxa exhibiting two scales of clustering were modelled as Thomas double cluster processes on a homogeneous background, and as single Thomas cluster processes on a heterogeneous background, as follows (Extended data Table 2):

1. The PCF was plotted, and ranges for the two different scales of clustering were found. For example, the small-scale cluster may be $0 < r < 0.5\text{m}$, and the large-scale cluster $0.5\text{m} < r < 1.5\text{m}$.
2. The large-scale cluster model was fitted.
3. The parameters of the large-scale single cluster model were used as parameters for the large-scale clusters of the double cluster model.
4. Nearest-neighbour functions were calculated and compared to the parameters of the different-scaled clusters to test for nestedness.

Comparison between and within taxa

To assess whether *Fractofusus* spatial distributions could be similarly modelled on all three bedding planes, the best-fit model from each surface was fitted to the other two surfaces. Simulation envelopes and p_d -values were used to evaluate fit (Fig. 2b, Extended data Table 3).

The uniqueness of each taxon's spatial distribution was assessed by fitting the best-fit models for high abundance taxa (*Fractofusus*, *Charniodiscus*, *Primocandelabrum*) onto each other. Low-abundance taxa (Charniids, *Thectardis*) were excluded from this comparison because they yield large simulation envelopes, and consequently very different models fit within the generated envelopes.

Size classes

The *Fractofusus* size data from the H14 surface permitted investigation of interactions between *Fractofusus* specimens of different sizes. To determine whether there was a dependency between spatial distribution and specimen size, the mark correlation function was calculated^{17,51} and compared to the simulation envelope produced from 99 Monte Carlo simulations (Extended data Fig. 3a).

The most objective way to resolve the number and range of size classes in a population is by fitting size-frequency distribution data (the natural log of the variables-lengths, widths, and the bivariate case of lengths multiplied by width) to various models, followed by comparison of (logarithmically scaled) Bayesian information criterion (BIC) values,⁷ which we performed in R using the package MCLUST.⁵² The number of populations thus identified was then used to define the most appropriate size classes. A BIC value difference of >10 corresponds to a “decisive” rejection of the hypothesis that two models are the same, whereas values <6 indicate only weakly reject similarity of the models.⁵⁹

Once defined, the spatial distributions for each size class were analyzed using the techniques described in the model fitting section (Methods: Model fitting). Although it was necessary to set firm boundaries for each size class, the populations are normally distributed and therefore overlap. As a result, the largest individuals of the small population are grouped within the middle size class, while some of the smallest of the medium population are included within the small size class.

Using this information, further analyses were performed to consider the spatial relationships between individual size classes. The PCF between each size class was determined, and the best-fit shared parent (SP) and linked cluster models (LCM) were fitted (Extended data Table 5, Extended data Fig. 4c,d), and the fit of each model assessed. SP models describe the pattern when two clustered size classes both cluster around an (undefined) point or area, such as the effect of two different heterogeneous soil effects on tree

growth.⁵³ Linked cluster models arise when one size class clusters around another size class, for example when tree saplings cluster around their parent.⁵⁴ The procedure behind model fitting was similar to the single group/size class (univariate) case, but instead of single groupings, two size-classes (bivariate) PCF were used instead:

1. The best-fit Thomas cluster processes were found for each of the size classes (SP and LCM).
2. The single size class parameters for each size were input to the model classes (both models for the SP model and only the parent model for LCM).
3. The best-fit model was fitted to the PCF and L functions.
4. If the model fit was poor (errors >0.025), then the model was fitted using the PCF and then the L function. If neither were a good fit, then the spatial scale that the model was fitted to was reduced, so that a good model could be found for at least part of the spatial scale.
5. The model was checked using 99 Monte Carlo simulations, p_d -values, and by comparing the univariate parameters to the bivariate model parameters.

Isotropy analysis

To assess whether non-random behaviour was stronger in any particular direction (i.e., exhibited isotropy), density plots of the K measure^{5, 55} were used to calculate the normalized density in each direction around each point (Fig. 3 and Extended data Fig. 3c), where normalized values of 1 indicate random distribution (homogeneous Poisson process), vs <1 (segregation) and >1 (aggregation). The plots are produced by calculating the average of all the vectors that join all pairs of points over different realisations of the point process. Each point in turn is positioned on the plot centre, then a vector is drawn to every point. The resulting vector scatter plot (also known as a Fry plot) is then smoothed.

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Extended Data Figure 1: Map and simplified stratigraphic column showing the position of studied bedding planes with bedding plane maps of *Fractofusus*. **a**, Newfoundland, Eastern Canada. Dashed area indicates region of interest in B. **b**, The Avalon and Bonavista Peninsulas, eastern Newfoundland. Locations of the bedding planes are indicated. **c**, Stratigraphic column (not to scale) compiled of information from the Avalon and Bonavista Peninsulas; lithological units in each region are treated as correlative in this study, but work is ongoing to determine the validity of this assumption. The ‘E’ surface at Mistaken Point has been dated to 565 ± 3 Ma¹². There are currently no available radiometric dates from the Bonavista Peninsula. Maps of *Fractofusus* positions on **d**, the ‘D’ surface, **e**, the ‘E’ surface and **f**, the H14 surface. In Fig. e the largest specimens in light blue, medium specimens in mid blue and smallest specimens in dark blue.

Extended Data Figure 2: Retrodeformation calculations on the Mistaken Point surfaces. Plots of the lengths versus widths of discs from **a**, the ‘D’ surface, Mistaken Point and **b**, the ‘E’ surface Mistaken Point. The gradient of the line defines the retrodeformation factor, which for ‘D’ surface is 1.35 ± 0.11 ($R^2 = 0.92$), and for ‘E’ surface is 1.71 ± 0.08 ($R^2 = 0.75$). **c**, *Fractofusus* PCF on the ‘E’ surface with (solid black line) and without (dashed black line) retrodeformation. The grey shaded area depicts the boundary of 99 Monte Carlo simulations for the model which provided the best-fit model to the retrodeformed data, which has a good fit on the non-retrodeformed data ($p_d = 0.60$)

Extended Data Figure 3: Size distribution analysis of *Fractofusus* for the H14 surface. **a**, Size-frequency distributions for *Fractofusus*, and **b**, the results of Bayesian Information Criterion^{52,53} (BIC) (univariate data). Triangles and squares correspond to models assuming equal and unequal variance respectively. High BIC values correspond to a good model fit, so the best-fit model is a three component equal variance model using log-normalized length data. **c-d**, Rose diagrams plotting the directional orientation of the different size classes of

Fractofusus on H14 surface showing **c**, Large size class (<11.0cm), **d**, Intermediate size class (5.5-11.0cm) and **e**, Small size class (<5.5cm). The angles of the *Fractofusus* central axis relative to North (0°). There is no strong orientation preference for any of the size classes.

Extended Data Figure 4: Distance measures for the size data from H14 surface. For all plots the x-axis is the inter-point distance between organisms in metres. **a**, Mark correlation function,⁵ where 1 corresponds to a lack of correlation of size, such that *Fractofusus* size is independent and identically distributed. <1 corresponds to a positive dependency (in contrast to PCF) and >1 corresponds to a negative dependency. Fig. a shows that small *Fractofusus* on the H14 surface (<0.3cm) are more likely to be found near each other than expected by random. **b**, The H14 surface PCF (solid line) showing the model that fits the data best, a double Thomas cluster model (dotted line, $p_d=0.89$), and the simulation envelope for 99 Monte Carlo simulations (grey shaded area). PCF for the best-fit models for the bivariate size-classes of *Fractofusus* on H14 surface showing: **c**, Linked cluster model for small with medium size classes ($p_d=0.74$) and **d**, Linked cluster model for medium with large size class ($p_d=0.66$). **e**, The PCF of the largest size class of H14 (solid line), showing the CSR Monte Carlo simulation envelope in grey, with the 'D' surface PCF (dotted line, $p_d=0.56$). **f**, Nearest neighbour distances (solid line, $p_d=0.01$) with CSR Monte Carlo simulation envelope in grey.

Extended Data Figure 5: Artistic reconstruction of *Fractofusus* on the H14 surface, Bonavista Peninsula. Artwork by C.G.K. The bottom right features a large *Fractofusus* around which there are five to eight medium specimens clustered. Each of the medium specimens also has small specimens clustered around them. The small specimens therefore form an independent double cluster pattern, that is, clusters of clusters.

Extended Data Table 1: Best-fit univariate cluster models. For the heterogeneous backgrounds, the moving window radius is 0.5m using the same taxon density as the taxon being modelled. $p_d = 1$ corresponds to a perfect fit of the model on the data, while $p_d = 0$ corresponds to no fit. The error function of the best-fit model gives the fraction of the total sum of squares for the transformed empirical PCF which are not explained by the model.

Extended Data Table 2: Best-fit univariate double cluster models. Large-scale clusters are determined for the univariate cluster then input into the model, and the small-scale clusters are determined in the double cluster analysis. $p_d = 1$ corresponds to a perfect fit of the model on the data, while $p_d = 0$ corresponds to no fit.

Extended Data Table 3: The best-fit double Thomas cluster models fit onto other taxon $p_d = 1$ corresponds to a perfect fit of the model on the data, while $p_d = 0$ corresponds to no fit. Note, that while these numbers may seem low (such as the ‘E’ surface fit), they need to be considered in context of the PCF graph (Extended Data Fig. 2b), which clearly shows a good fit to the data, with the small fluctuations of the observed PCF around the model PCF.

Extended Data Table 4: Best-fit univariate cluster models on heterogeneous backgrounds for ‘E’ surface taxa. Univariate clusters, either fitted to the small scale (S) or large scale (L) were modelled on different backgrounds defined by the density map of all taxonomic groups, or Random for charniid. C: Thomas cluster on homogeneous background. CH: Thomas cluster on heterogeneous background. For the heterogeneous backgrounds, the moving window radius is 0.5m since that radius produced the best-fit for Charniids: Heterogeneous Cluster model on a background density constructed from all species: (CH_{all}); Ivesheadiamorphs (CH_{Ive}), *Fractofusus* (CH_{Frac}), *Charniodiscus* (CH_{Cha}), *Primocandelabrum* (CH_{Primo}). CSR on heterogeneous background (H). *Bradgatia* (H_{Bra}),

715 Lobate Discs (H_{Lob}), *Thectardis* (H_{The}), Charniid (H_{Char}). $p_d = 1$ corresponds to a perfect fit
716 of the model on the data, while $p_d = 0$ corresponds to no fit. The H14 surface did not possess
717 enough non-*Fractofusus* specimens to perform similar analyses. NA: not applicable.

718

719 **Extended Data Table 5: Models for bivariate analysis between different size classes of**
720 ***Fractofusus* on the H14 surface.** SP refers to shared parents models, and LCM refers to
721 linked cluster models. $p_d = 1$ corresponds to a perfect fit of the model on the data, while $p_d =$
722 0 corresponds to no fit. The large size class was randomly distributed, but was approximated
723 by a cluster model, which was required for input into Programita.⁹

724